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After biocontrol: Assessing indirect effects of insect releases

Julie S. Denslow [a,*], Carla M. D'Antonio [b]

[a] *Institute of Pacific Islands Forestry, USDA Forest Service, 23 E. Kawili St., Hilo, HI 96720, USA*
[b] *USDA-ARS, 920 Valley Road, Reno, NV 89512, USA*

Abstract

Development of biological control agents for weeds has been motivated by the need to reduce the abundance and distribution of a pest plant where chemical and mechanical control were not cost effective. Primary objectives have been direct reduction in abundance of the target and, secondarily, the increase of desirable species. Recently, wildland weeds have become a focus of biological control projects. Here, desired outcomes include both reduction of the target and indirect effects of increased diversity and abundance of native species and restoration of ecosystem services. However, goals and benefits of biocontrol programs are not always well-articulated and direct and indirect impacts are not easily predicted. We evaluated the extent to which several successful biological control projects for weeds of rangelands and waterways measured indirect impacts on invaded ecosystems. We also examined biocontrol of a wildland pest tree for which the principal objective is restoration of ecosystem services. We found few quantitative assessments of the impacts of pest plant reduction on community composition or ecosystem processes. All examples documented variation in the impacts of agent(s) across the invasive range of the target plant as well as variation in impacts on the invaded ecosystem. However, without appropriate quantitative information, we cannot evaluate site characteristics that may influence vegetation responses. Most successful weed management programs integrated the use of biocontrol agents with other weed management strategies, especially modifications of disturbance and competing vegetation. Discussion and evaluation of responses of nontarget species would improve our understanding of the context-specificity of outcomes.
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1. Introduction

Development of biological control agents for weeds has been motivated by the need to reduce the abundance and distribution of a pest plant where chemical and mechanical controls were not cost-effective (Harris, 1993; Pemberton and Turner, 1990). Widespread weeds of uncultivated lands, including rangeland weeds, such as *Hypericum perforatum* L. (Harris et al., 1969), *Euphorbia esula* L. (Harris, 1993), and *Opuntia* spp. (Moran and Zimmermann, 1984) are good examples. Historically, the primary objective of weed biological control has been the direct reduction in density, cover, and range of a target weed that has suppressed desirable forage species or was toxic or unpalatable to livestock. A secondary objective, therefore, has been to improve pasture or rangeland productivity or to promote the replacement of the target with something more desirable. Target selection has been influenced strongly by client groups, such as cattlemen's associations, whose sustained interest has been critical to the continued development of such publicly funded projects. Yet increasingly, public, government, and scientific communities in the USA have become skeptical of biocontrol programs because of their potential to cause both direct and indirect nontarget impacts (e.g., Beardsley, 1997; Louda et al., 1997, 2003a,b, 2005; McEvoy and Coombs, 2000; Simberloff and Stiling, 1996). Such skepticism

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* Corresponding author. Fax: +1 808 933 8120.
 E-mail address: jdenslow@fs.fed.us (J.S. Denslow).

raises the question of how clearly the goals and benefits of biocontrol programs are articulated in advance and the degree to which direct and indirect impacts can be predicted and measured.

With increasing appreciation of the impact of invasive plants on native ecosystems, and heightened value placed on wildlands, weeds of natural areas recently have become an important focus of biological control projects. As is the case for rangeland weeds, the potential effectiveness of biological control over large areas of poorly accessible terrain is attractive economically (Malecki et al., 1993). Moreover, biocontrol agents are usually highly host-specific and thus produce fewer non-target impacts than does widespread use of chemical and mechanical control methods. Recent projects for control of *Melaleuca quinquenervia* (Cav.) Blake in the Florida Everglades, *Lythrum salicaria* L. in the northern wetlands, and *Tamarix* spp. along western stream courses are driven by perceived threats these species pose to ecosystem services and native species. Desired outcomes of the biological control of such wildland weeds, therefore, include both direct reduction of the target as before as well as indirect effects such as increased abundance of native species, increased species diversity, restoration of vegetation structure, and restoration of ecosystem processes and services, such as water yield, that presumably had been provided by the pre-invasion community (Harris, 1993; Lesica and Hanna, 2004). Expansion of use of biological control to target wildland weeds, therefore, has increased the potential list of benefits of biocontrol while simultaneously increasing the complexity of measuring, monitoring, and modeling responses and potential benefits.

In the current climate of skepticism, it is increasingly important for scientists to quantify ecological responses to control activities and for biocontrol projects to be developed as part of integrated weed management and restoration programs, rather than as stand-alone projects. For meaningful risk/benefit analyses to be conducted, ecologists must be able to assign probabilities to outcomes of insect releases. We should be able to estimate not only the probabilities of the successful establishment of the released agent and subsequent depression of the target, but also the probabilities associated with desired community and ecosystem responses, particularly as they relate to the ultimate management goal that motivated control in the first place (Fig. 1).

Our goal in this paper is to evaluate the extent to which several seemingly successful biological control projects measure the full range of impacts of the biocontrol agents on the invaded communities and ecosystems. We are interested specifically in what was monitored after release of the control agent(s) and the extent to which indirect impacts (e.g., Fig. 1) were measured and ultimate goals achieved. We do not focus on feeding of the agent on nontarget plant species since that has been
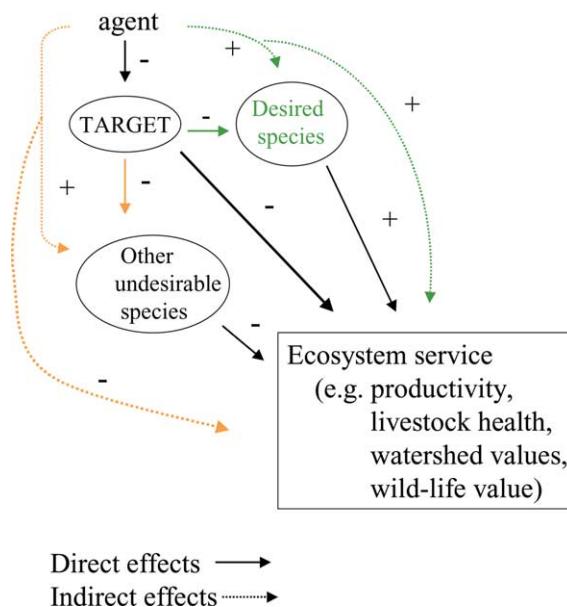

Fig. 1. Two potential pathways through which indirect effects could develop as a result of a biocontrol introduction. The green pathway demonstrates a desired indirect effect whereby suppression of the target releases desired species and thereby improves ecosystem services. The orange pathway demonstrates an undesirable outcome whereby control of the target releases other undesirable species, which continue to suppress ecosystem services. If this response is anticipated, then control of other species must occur simultaneously with target control.

covered well elsewhere (e.g., Louda et al., 2003a,b; McEvoy and Coombs, 2000; Pemberton, 2000; Simberloff and Stiling, 1996; and others). Rather, we evaluate how fully control projects measured desired or even undesirable outcomes and the extent to which true benefits were realized even with only partial control of the pest. Fig. 1 provides a conceptual presentation of potentially desirable and undesirable outcomes. Such information would be useful to determine whether a release is justified when full control is not expected. We have reviewed only successful projects, defined as those for which authors report noticeable reductions in the cover or distribution of the pest plant. We sought insights into ways in which to better measure community and ecosystem responses to biocontrol releases. Ultimately, such information should improve the utility of risk/benefit analyses as well as the outcomes.

2. Materials and methods

We consulted the published literature on nine biocontrol projects for which some measure of success in reducing the density, range, or abundance of the target pest has been claimed. Projects were selected from those listed in Julien and Griffiths (1998) for which one or more biological control agents released at least 10 years ago were described as substantially reducing the cover of the target weed. The project list includes target weeds of

rangeland as well as wildlands and herbaceous, woody, and aquatic species (Table 2). Examples come from many countries, although our primary focus has been on weeds targeted within the United States. In many cases, multiple agents have been targeted to control a single plant species and in others a single species has effected control. We consulted published references listed in Julien and Griffiths (1998), as well as subsequent publications and current web sites. We were not able to follow-up on citations recorded by Julien and Griffiths (1998) as "personal communication," although it is clear that considerable valuable information resides in laboratory records and with individual researchers and needs exposure. In addition to these published examples, we discuss an ongoing project in a wildland setting from the western United States with which we are familiar; it provides important insight into assessment and monitoring considerations where the desired result is clearly a change in ecosystem processes.

3. Results

Table 1 lists a range of impacts described in the literature with associated codes, which we then use to summarize published findings in Table 2. Where a citation claimed simply "substantial control" or similar phraseology, we assumed this meant reduction of cover or biomass (COV) unless reduction of density was specified. The history of most planned introductions of biological control agents describes highly variable results, including failure to establish; establishment but no effective control accomplished; initial control followed by gradual recovery of the target weed; patchy effects across

Table 1
Observed direct and indirect effects of biological control of target weeds with abbreviation codes used in Table 2

	Code
Direct effects on target weed	
Defoliation	DEF
Reduced seed or fruit set	SS
Reduced cover or biomass	COV
Reduced density	DEN
Reduced habitat range	HAB
Reduced geographic range	GEO
Reduced rate of spread	SPR
Reduced growth or reproduction of nontarget species	NTG
Reduced density of nontarget species	NTDEN
Indirect effects on the ecosystem	
Increased economic productivity	ECN
Increased abundance of native species	NAT
Increased abundance of exotic species	EXO
Increased species richness or diversity	DIV
Restored ecosystem processes (disturbance frequency, nutrient processes, hydrology)	ECS
Restored community or vegetation structure	STR
Improved management effectiveness	MGT

habitat and geographic ranges; as well as strong, long-lasting control (Julien and Griffiths, 1998). While direct impacts of control agents were generally better documented than indirect impacts, lack of quantitative data on the outcome of most control efforts hindered our ability to establish strict criteria for assignment of impacts in Table 2.

The lack of quantification in evaluation of outcomes and the lack of clarity in definitions of success that typify biocontrol programs have been noted by Crawley (1989) and others (see McEvoy and Coombs, 1999). Likewise, we found great variability in what was measured and how success was defined. In particular, we found relatively few quantitative assessments have been made of the impact of pest plant reduction on the invaded ecosystem (Indirect Impacts, Table 2). The few studies with such information generally addressed growth or cover responses of native and exotic species, improved productivity of rangeland, or consequences for management, but quantitative data were rare. We also found little attention to community diversity or structure or to impacts on ecosystem processes such as fire frequency, hydrology, or nutrient dynamics. Since these were rarely the primary motivations for the initiation of biocontrol projects on rangeland weeds, it is not surprising that post-control evaluations did not address them. Yet they are important potential outcomes that could affect the direction and intensity of management of the affected ecosystems.

3.1. Pasture and rangeland weeds

3.1.1. St. Johnswort

Hypericum perforatum L. (St. Johnwort) was a major rangeland weed of the western states and British Columbia. In addition to its toxicity to cattle and humans, it was a serious weed of pasture and range, occurring across two million acres in Western United States and Canada before the advent of effective biological control (Harris, 1988, 1993; Harris et al., 1969). Two beetles, *Chrysolina hyperici* (Forster) and *C. quadrigemina* (Suffrian) (Coleoptera: Chrysomelidae), released in 1945–1950, were credited with reducing the weed to 1% of its former density in most habitats, although dense stands remain where frost limits the length of the beetle egg-laying period (Harris and Maw, 1984). Reported responses of other plant species to weed suppression in invaded grasslands were varied. In California, Huffaker and Kennett (1959) monitored the reduction in cover of the target plant and the simultaneous increase in desirable forage species for four stands in which the beetles had been released. Their studies showed no effect on other noxious weeds, but did record an increase in exotic pasture grasses. At that time, these replacement species were not of ecological concern so project goals were met. Huffaker and Kennett (1959) also note a 35% increase in plant diversity after control of *Hypericum*. Their study is

Table 2
Recorded impacts of successful biological control agents on target weeds and on invaded ecosystems[a]

Target weed	Origin	Invasive range	Habitat/impact	Primary agents/release dates	Effects	References[b]
Rangeland Weeds						
Ageratina riparia (Regel) King and Robinson (Asteraceae) mistflower	Mexico	Hawaii, Australia, S. Africa	Rangeland in moist and dry areas, forest; Reduced rangeland productivity	*Entyloma ageratinae* Barreto and Evans (Ustilaginales) 1975–1989 *Oidaematophorus beneficus* Yano and Heppner (Lepidoptera) 1973 *Procecidocares alani* Steyskal (Diptera) 1945–1986	Direct: DEN, COV, HAB, GEO. Indirect: EXO, ECN	Trujillo (1985), Morin et al. (1997)
Carduus nutans Linnaeus (Asteraceae) musk thistle	Europe, Asia	Australia, New Zealand, North America, Argentina	Rangeland. Reduced cover of forage species; reduced pasture productivity	*Rhinocyllus conicus* (Fröhlich) (Coleoptera) 1969–1981	Direct: DEN, COV, GEO, SS, NTG; Indirect: EXO, NAT, ECN, MGT	Harris (1984, 1993), Louda et al. (1997, 2003a,b), Rees (1977), Kok and Surles (1975), Kok and Pienkowski (1985)
Euphorbia esula L. (Euphorbiaceae) leafy spurge	Eurasia	United States and Canada	Rangelands, grasslands reduces productivity, replaces desirable species, toxic to cattle	Various *Aphithona* species (Coleoptera) including *A. cyparissiae, A. czwalinai, A. flava, A. lacertosa, A. nigriscutis*	Direct effects: COV, HAB, DEN. Indirect effects: NTG, MGT, DIV, NAT, ECN	Bangsund and Leisritz (1991), Lesica and Hanna (2004), Lym (1998), Lym and Nelson (2000, 2002)
Hypericum perforatum Linneaus (Clusiaceae) St. John's wort	Asia Minor, Europe, northern Africa	Australia, Chile, N. America (esp CA), New Zealand, S. Africa	Rangeland and native grasslands. Reduces econ. productivity; toxic to cattle, competes with native species; widespread	*Chrysolina hyperici* (Forster) (Coleoptera) 1930–1980 *Chrysolina quadrigemina* (Suffrin) (Coleoptera) 1939–1990	Direct: COV, DEN, GEO, HAB, NTG Indirect: ECN, NAT, STR, EXO	Briese (1985), Campbell and McCaffrey (1991), Harris (1988), Harris and Maw (1984), Harris et al. (1969), Huffaker and Kennett (1959)
Opuntia spp. incl. *C. aurantiaca* Lindley, *O. cordobensis* Spegazzini, *O. elatior* Miller, *O. ficus-indica* (L.) Miller, *O. imbricata* (Haworth) DC, *O. lindheimeri* Engelmann, *O. littoralis* (Engelmann) Cockerell, *O. oricola* Philbrick, *O. streptacantha* Lemaire, *O. stricta* (Haworth) Haworth, *O. tomentosa* Salm Dyck, *O. tricantha* (Willdenow) Sweet, *O. tuna* (L.) Miller, *O. vulgaris* Miller Prickly pear cacti	Neotropics, including Caribbean, SW United States, and Mexico	Australia, S. Africa, Hawaii, India, Indonesia, Nevis, Cayman Is., Antigua, New Caledonia, SW United States, Sri Lanka, Mauritius, Kenya, Israel, Pakistan, Madagascar, St. Helena	Rangeland. Reduced cover of pasture grasses and reduced range quality	*Cactoblastis cactorum* (Bergroth) (Lepidoptera) 1926–1994 *Dactylopius opuntiae* (Cockerell) (Hemiptera) 1921–1957	Direct: DEN, HAB, GEO, COV, NTG. Indirect: NAT, ECN, MGT	Goeden and Ricker (1981). Johnson and Stiling (1998), Moran and Zimmermann (1991), Zimmermann and Moran (1991)

Senecio jacobaeae Linnaeus (Asteraceae) tansy ragwort	Eurasia, N. Africa	Australia, New Zealand, North America	Rangeland/coastal prairie/cutover forest lands, nonirrigated pastures, woodland pastures; Alkaloids cause liver damage and death to cattle and horses; reduced range quality and productivity	*Longitarsus jacobaeae* (Waterhouse) (Coleoptera) 1969–1987 *Tyria jacobaeae* (Linnaeus) (Lepidoptera) 1930–1993	Direct: HAB; DEF, DEN; COV, GEO, NTG. Indirect: ECN, NAT, EXO	Coombs et al. (1991, 1996), Diehl and McEvoy (1990), Gruber and Whytemare (1997), Harris et al. (1978a,b), McEvoy et al. (1991), McEvoy and Coombs (1999), Pemberton and Turner (1990)
Aquatic weeds						
Eichornia crassipes (Martius) Solms-Laubach (Pontederiaceae)	South America	Widespread; tropical and warm temperate climates;	Freshwater, rivers, canals, lakes Water flow, oxygen depletion, mosquito habitat	*Neochetina bruchi* Hustache (Coleoptera) 1972–1996 *Neochetina eichorniae* Warner (Coleoptera) 1971–1996	Direct: COV, SS, COV, HAB, GEO; SPR. Indirect: MGT	Beshir and Bennett (1985), Center and Durden (1986), Gordon (1998)
Alternanthera philoxeroides (Martius) Griesebach (Amaranthaceae) alligator weed	South America	Australia, New Zealand, China, Thailand, SE United States	Freshwater rivers, lakes; shorelines Water flow, oxygen depletion, suppression of native species	*Agascles hygrophila* Selman and Vogt (Coleoptera) *Amynothrips andersoni* O'Neill (Thysonoptera) *Arcola malloi* (Pastrana) (Lepidoptera)	Direct: DEF, COV, HAB. Indirect: NAT, MGT, ECS, EXO, DIV	Sailer (1972), Coulson (1977), Julien (1981), Buckingham (1996)
Pistia stratiotes L. (Araceae) water lettuce	Cosmopolitan tropical and sub-tropical	AU, Africa, PNG, SAf, US	Freshwater rivers, lakes. Water flow, oxygen depletion, mosquito habitat	*Neohydronomus affinis* (Hustache) (Coleoptera)	Direct effects: COV, SPR, HAB. Indirect effect NAT, EXO	Cilliers et al. (1996), Chikwenhere (1994), Harley et al. (1990)
Wildland weeds						
Tamarix spp. [Tamaricaceae] *T. ramossisma* Ledeb, *T. chinensis* Luor., *T. parviflora* DC. tamarix, saltcedar	Asia, Medit. Europe, N. Africa	Western USA, Australia	River corridors, reservoir margins, springs, seeps	*Diorhabda elongata* Brulle (Chrysomelidae)	Direct effects: COV. No indirect effects have yet been published	Dudley et al. (2001)

[a] References are coded by the nature of the data they provide (see Table 1 for codes). Taxonomic nomenclature, origin, and invasive range are from Julien and Griffiths (1998). Invasive ranges are for those countries releasing biocontrol agents.

[b] See Julien and Griffiths (1998).

notable for being one of the earliest studies to quantify vegetation responses to biocontrol of a target weed. After the release of biocontrol agents on St. Johnswort in Idaho, Campbell and McCaffrey (1991) described its replacement by other noxious weeds, including *Centaurea solstitialis* L., *Convolvulus arvensis* L., and *Taeniatherum caput-medusae* (L.) Nevski, even where rangelands were ungrazed. These findings emphasize the need to take context-specificity into account when evaluating potential responses to weed control, and the need to weigh the negative impact of one pest species against that of others that may replace it. While one weed may be easily reduced by a biocontrol agent, its potential replacement may be a less easily controlled noxious species. Whenever possible, vegetation management programs should address the control of multiple pest plants.

3.1.2. Tansy ragwort

Senecio jacobaea L. (tansy ragwort) is, similarly, a prairie and rangeland weed that reduces economic productivity because it suppresses desirable forage species and is toxic to horses and cattle (Harris et al., 1984). Control for this species began in the 1970s and was considered successful by the late 1980s (Coombs et al., 1991, 1996). It is currently being controlled largely by cinnabar moth, *Tyria jacobaeae* (L.) (Lepidoptera: Arctiidae), and ragwort flea beetle, *Longitarsus jacobaeae* (Waterhouse) (Coleoptera: Chrysomelidae), with the efficacy of the control agent depending on the geographic location. West of the Cascades, the beetle is the more effective control agent (McEvoy and Coombs, 1999). Harris et al. (1978a,b) observed that in western Canada where the *Senecio* stands are dense, the growing season long, and summer moisture supply good, the moth is unable to reduce plant densities. It is a more effective agent in Eastern Canada where shorter growing seasons reduce carbon reserves and thus vegetative reproduction. In Oregon, McEvoy and Coombs (1999) experimentally manipulated disturbance, competition, and the presence of the two control agents to show that a multi-pronged approach produced effective and lasting control, with the flea beetle being the most important control agent. Their study, which combined a mixture of field experiments and modeling, emphasized the conditional nature of community responses and the importance of managing the weed in the context of the entire ecosystem. McEvoy and associates also described direct nontarget impacts by cinnabar moth feeding on a native *Senecio* (Diehl and McEvoy, 1990), and they documented the recovery of an endangered native forb after control of *Senecio* on a nature preserve (Gruber and Whytemare, 1997). They also found increases in standing biomass of the vegetation in response to *S. jacobaea* control (McEvoy et al., 1991).

The importance of increased competition from background species and reduced soil disturbance to weed

suppression has been highlighted also by Pemberton and Turner (1990), who examined the consequences of reduction in *Senecio* in invaded grasslands in northern California. In their study sites, *Senecio* was replaced in coastal prairies by a mixture of native species. Where pastures were heavily grazed, however, *Senecio* remained an important part of the vegetation, although reduced somewhat in cover. In a less heavily grazed pasture, *Senecio* was replaced by a mixture of desirable forage species as well as by undesirable exotic thistles. While pasture productivity was not measured directly, the authors state that, in comparison to its pre-control condition, the pasture regained its utility, although the presence of exotic thistles reduced productivity (Pemberton and Turner, 1990). The results suggest that livestock grazing management is an important component to the achievement of desirable target vegetation.

3.1.3. Thistles

The weevil, *Rhinocyllus conicus* (Frölich) (Coleoptera: Curculionidae), was introduced to reduce reproduction of exotic rangeland thistles, especially the musk thistle, *Carduus nutans* L. While the agent has become widely distributed, its effects on seed production vary. Impacts on the first, terminal inflorescences of the season can be high with a large proportion of seed consumed or damaged, but the impacts on late-season lateral buds can be considerably less (Kok and Surles, 1975; Rees, 1977). Nevertheless, Kok and Surles (1975) observed 90% reduction in thistle densities, including complete elimination in some Virginia plots, followed by revegetation with other vegetation including grasses. Moreover, Harris (1984) reports that in Saskatchewan the weevil has reduced dense stands of the musk thistle from a category 4 weed (continuous thistles or >50 stands/ha) to a category 1 or 2 weed (1, no *C. nutans*; 2, scattered thistles or <1 stand/ha). Harris (1993), summarizing the history of this biocontrol agent, noted that once established, the thistle dominates pasture land, but in well-managed pastures in the presence of *R. conicus*, grasses return in about 3 years and continue to suppress the thistles. The weed persists along roadsides, in overgrazed or drought-stressed range, and in other disturbed areas, even in the presence of *R. conicus*, but is largely absent from well-managed range.

Rhinocyllus conicus is widely known for its direct impacts on nontarget plants, some of which are rare (e.g., Louda et al., 2005, 1998, 2003a,b). Hence, its release for biological control has been criticized and the benefits of its release must be weighed against the ecological costs incurred to nontarget species. *Rhinocyllus conicus* is now widespread, so further releases may not affect its distribution. However, it would seem unjustifiable to release agents, which have known nontarget impacts and for which large reservoirs of host plants remain on unmanaged land.

3.1.4. Leafy spurge

Euphorbia esula L. (leafy spurge) is a perennial, toxic weed that can reach 100% cover across a wide variety of habitats including floodplains, grasslands, and mountain slopes, especially across the Northern Great Plains, where it reduces the carrying capacity of the range (Bangsund and Leisritz, 1991). Successful biocontrol has been attained through the release of several species of root-feeding beetles in the genus *Aphthona* (Coleoptera: Chrysomelidae), each with specific habitat preferences characterized by different soil conditions (Harris, 1993). While impacts of the beetles are substantial, rate and effectiveness of control is improved by coupling biocontrol with a variety of other management techniques, including fall application of herbicides, grazing by sheep or goats, or tillage (Lym, 1998; Lym and Nelson, 2000, 2002; also see Caesar, 2005, on the role of interactions between microorganisms and insects on leafy spurge), the particular combination of management techniques tailored to individual site conditions. Site conditions also influence the impact of *Euphorbia* reduction on the invaded plant community. Lesica and Hanna (2004) compared the effects of *Aphthona* releases with control plots in two situations. They found that diversity of both native and exotic species increased following *Euphorbia* control on low-fertility sites, but not on sites with relatively rich soil previously treated with herbicides. While causes of these site differences in response to weed control were not determined, their study highlights the complexity of factors affecting community composition and responses to changes in species dominance.

3.1.5. Cacti

At least 46 species of Cactaceae have been identified as problem weeds and 65 species of insects and mites have been introduced to control them. The most effective have been species of the cochineal insect in the family Dactylopidae (Moran and Zimmermann, 1991) introduced against members of the genus *Opuntia*. Together with the cactus moth, *Cactoblastis cactorum* (Bergroth) (Lepidoptera: Pyralidae), substantial reduction in individual infestations have been reported for some species and situations. For example Julien and Griffiths (1998), reviewing reports from Hawaii, recorded reduction in cactus cover in lowland arid sites, but insignificant control above 900 m. Although no data are presented on response of desired vegetation to control, reduction in cactus cover is assumed to lead to increases in desired species. Here, too, the importance of integrated pest management is seen as the key to effective management. On Santa Cruz Island, California, biocontrol of *Opuntia* spp. together with improved competition from native grassland species through reduced ungulate grazing pressure resulted in an increase in native and desirable exotic pasture species (Goeden and Ricker, 1981). In South Africa, strategic application of herbicides were recommended to permit persistence of populations of the agent and maintain the weed at tolerable densities (Zimmermann and Moran, 1991). The authors suggested that these protocols should recognize differences in effectiveness of the agent under different climate conditions (Zimmermann and Moran, 1991). Nevertheless, they emphasized that the potential for increased density and spread of cactus weeds has probably been over estimated in South Africa. They suggested that improved land management coupled with repeated inoculation of infestations using existing agents would be sufficient to keep populations of the weed at tolerable levels.

3.1.6. Mist flower (Hamakua Pa'makani)

The biological control of mist flower (*Ageratina riparia* (Regel) King and Robinson) in Hawaii has been one of the most successful programs on record (Morin et al., 1997). Introduced around 1925, its prolific seed production in cool, moist environments led to its domination in both upland pasture and forest floor habitats. The combination of a fungus (*Entyloma ageratinae* Barreto and Evans; Ustilaginales: Tilletiaceae), a gall fly (*Procecidochares alani* Steyskal; Diptera: Tephritidae), and a plume moth (*Oidaematophorus beneficus* Yano and Heppner; Lepidoptera: Pterophoridae) have reduced the population across its range of habitats to scattered stunted individuals (Morin et al., 1997; Trujillo, 1985, 2005). Success of control is attributed in part to the complementarity of the agents, the dipteran being more effective in dry areas and the fungus more effective in cool, moist habitats. No quantitative assessments of indirect impacts of decline in *Ageratina* have been undertaken, although sequential photographs document its replacement with a variety of introduced pasture grasses (Trujillo, 1985, 2005). While many of these grasses provide valuable forage for livestock, they can also cause problems for native species (D'Antonio et al., 1998; Hughes et al., 1991; Smith, 1985). In one forest where *Ageratina* once dominated, an exotic shade-tolerant grass now competes with native species (Denslow et al., unpublished). Thus, in the case of forested habitats, it is not clear whether the indirect benefits from *Ageratina* control, including increased growth and establishment of native understory species, have been realized.

3.2. Aquatic weeds

The motivation for development of biocontrol on weeds of lakes, impoundments, canals and rivers, such as *Eichhornia crassipes* (Martius) Solms-Laubach, *Althernathera philoxeroides* (Martius) Griesbach, and *Pistia stratiotes* L., reflects the broad impacts of these species and others on ecosystem processes as well as on

community structure and species diversity. Water weeds are implicated in oxygen depletion, alteration of water flow, sediment deposition, changes in water chemistry as well as in competition with native plants, loss of fish stocks, and increases in the mosquito vectors of malaria (Chikwenhere, 1994; Cilliers et al., 1996; Coulson, 1977; Gordon, 1998; Harley et al., 1990). The necessity of broad, integrated plant-community management to restore desired community and ecosystem properties is particularly evident in the history of biocontrol of aquatic weeds. Control of alligatorweed, principally by the flea beetle *Agasicles hygrophila* Selman and Vogt (Coleoptera: Chrysomelidae) was one of the early successes in the use of biological control agents (Coulson, 1977). Its success highlighted not only the power of a defoliator to reduce the vigor and biomass of an important aquatic weed, but also the importance of competition with other aquatic plants, stresses from other native and introduced insect herbivores, management of water levels, and coordination with use of herbicides and mechanical control (Buckingham, 1996; Coulson, 1977; Julien, 1981). The necessity of "environmental engineering at the ecosystem level" was noted early by Sailer (1972) recognizing the need to manage a suite of aquatic species, any one of which could expand to exploit the resources freed by the reduction of alligatorweed. Similarly, Chikwenhere (1994) described the rapid (<16 mo) substantive (80%) reduction in *Pistia* cover by the beetle *Neohydronomus affinis* Hustache (Coleoptera: Curculionidae) in Zimbabwe, but observed that *Pistia* rapidly was replaced by other water weeds including *Eichhornia*. Cilliers et al. (1996) document dramatic control of *Pistia* by the same agent in Kruger National Park, South Africa, but note that plant cover also fluctuates with water flow and that populations are better controlled by combining biocontrol with judicious use of herbicides to new populations to keep the seed bank small and reduce the impact of rotting vegetation on oxygen levels in the water. *Neochetina* beetles (*Neochetina bruchi* Hustache and *N. eichhorniae* Warner Coleoptera: Curculionidae) provide good biomass reduction of waterhyacinth (*E. crassipes*) under flowing, high-nutrient conditions, but only if populations of the agent are allowed to develop sufficiently (Center and Durden, 1986). Thus, there is need for close coordination between managers using chemical and mechanical methods to control infestations of waterhyacinth and agencies releasing biocontrol agents at the same sites. These citations document the need for whole ecosystem management, with attention to the entire suite of aquatic weeds, the hydrology and nutrient status of the ecosystem, and the application of multiple management tools to effectively reduce the impacts of the weeds while minimizing such negative consequences of control as rotting vegetation and oxygen depletion.

3.3. Wildland weeds

Development of biological agents for the control of saltcedar (*Tamarix* spp.) has been underway for the past 15 years (DeLoach et al., 2003; Dudley et al., 2001; Lewis et al., 2003). The primary motivation for control of this weedy riparian tree is the water savings, which presumably will accrue to the water-starved western USA once the tree is controlled. Numerous estimates of *Tamarix* water use can be found in the literature (e.g., Shafroth et al., in press; Zavaleta, 2000), but close examination of individual studies reveals that effects of *Tamarix* removal are likely to vary depending on the nature of the replacement vegetation and on the particular site conditions (Shafroth et al., in press). Native cottonwood (*Populus* spp.), for example, can consume as much water as *Tamarix* (Dahm et al., 2002), so where it will replace *Tamarix*, water savings may not occur. A second motivation for *Tamarix* removal is improvement in habitat quality for wildlife in desert riparian corridors, but wildlife concerns are also controversial (Shafroth et al., in press). Beginning in 2000, the leaf beetle *Diorhabda elongata* Brullé (Coleoptera: Chrysomelidae) was released in six states; it has successfully established in at least four. Insufficient time has elapsed to permit a full evaluation of the program. Nevertheless, early indications suggest that only partial control has been achieved because the agents have not reproduced well in many sites (D. Bean, University of California, Davis, CA, personal communication; Lewis et al., 2003). An attempt now is being made to match agent biotypes with site characteristics (D. Bean, personal communication). In most other sites, *Tamarix* appears to endure repeated defoliation without mortality (T. Dudley and C. D'Antonio, personal observation). While mandated post-release monitoring includes measurement of the responses of both the target and co-occurring plant species, it does not include any estimation of benefits in water savings. Such estimates are time-consuming and require financing, but would indicate whether even partial control could result in water savings. Response of co-occurring vegetation, so far, appears to be minimal, but in many release sites abundant, problematic weeds such as tall whitetop (*Lepidium latifolium* L.) and Russian knapweed (*Acroptilon repens* (L.) DC) may take advantage of the decline of saltcedar (T. Dudley and C. D'Antonio, personal observations) pointing again to the importance of multi-species control and restoration programs. Scattered measurements of wildlife responses to control are also being conducted, but heterogeneity of the study sties and limited funding has hampered coordinated efforts to measure outcomes.

4. Conclusions

The above snapshots of large biocontrol projects reveal several common themes.

(1) Despite the varying quality of data, all of these examples document variation in the impacts of agent(s) across the invasive range of the target plant. Compensation for this variation often is made in the form of multiple agents targeted at specific climatic or habitat conditions. With better tools for predicting potential environmental ranges of agents (e.g., with the climate matching model, CLIMEX, e.g., Kriticos and Randall, 2001), our ability to target-specific habitat conditions for control will improve. Analyses of impacts at regional scales also improve our ability to select appropriate new release sites for agents. For example, Morin et al. (1997) used correlations between the relative efficacy of control and the temperature and moisture characteristics of release sites to develop a profile of the agents controlling *Ageratina* in Hawaii. The profile then was used to predict success probability in a new release program targeting *Ageratina* in New Zealand (Morin et al., 1997; also see Blossey et al., 2001 for projections of purple loosestrife control). Finally, regional evaluations of the impacts of agents provide insight into the importance of agents which, while not effecting complete control of the target pest, contribute to stress on its populations, as in the case of *C. quadrigemina* impacts on *Hypericum* in southeastern Australia (Briese, 1985).

(2) Successful weed management programs were frequently those that integrated the use of biocontrol agents with other weed management strategies, including modifications of grazing pressure, disturbance, tillage, and chemical control. Integrated weed management, coupling herbivory pressure from biocontrol agents with other forms of stress on the target weed is a productive combination and often recommended (e.g., Rees et al., 1996). The concept of combining top-down (including biocontrol) and bottom-up (e.g., resource supply, competition, and disturbance) control of weeds has been championed by McEvoy and Coombs (1999) and, although long recognized in the biocontrol community, nevertheless deserves greater attention during the planning of biocontrol projects.

(3) Discussions of the responses of invaded communities to target-plant reduction are scarce. Those reports that do exist suggest, not surprisingly, that results vary by site. Without appropriate, quantitative site information, however, it is impossible to evaluate site characteristics that may influence vegetation responses. Under some circumstances the release of native or otherwise desirable species follows suppression of the weed, sometimes leading to increased species diversity. Under other circumstances, biocontrol results in the replacement of the target weed by other noxious species. Our review suggests that management of livestock grazing pressures and disturbance as well as suppression of target weeds will affect native species abundance and diversity (e.g., Pemberton and Turner, 1990). Availability of propagules of desirable species also seems critical to their subse-

quent increase in abundance. Indirect effects of biocontrol on local plant communities, like removal of any dominant species, are driven by complex and poorly understood processes. However, such consequences should be considered before the initiation of a biocontrol project and anticipated as part of risk management following agent releases (Lonsdale et al., 2001). Biocontrol should be seen as part of a larger integrated vegetation management program and discussion of likely responses of nontarget species would improve our understanding of the context-specificity of outcomes. In this regard, innovative approaches using quantitative food webs are providing valuable insights into the role of biocontrol agents in larger communities (Henneman and Memmott, 2001; Willis and Memmott, 2005).

(4) Even in successful biocontrol projects, like those we review here, target plants are likely to remain part of the landscape due to disturbance and/or habitat heterogeneity. This means that even release of a successful biocontrol agent is unlikely to provide a long-term solution to management of the target pest. Rather, weed management is likely to require constant vigilance as alteration in climate, disturbance regimes, and land use patterns shift the balance of stresses on the target weed. If biocontrol projects are isolated from local or regional vegetation management decisions, they are less likely to result in sustained control.

(5) The spread and dominance of range weeds in many countries is the legacy of decades of mismanagement that has reduced competition from native species, provided habitat for noxious weeds, and efficiently spread seeds of pest plants over long distances (Mack et al., 2002). Improvements in range management to reduce input and inappropriate disturbance as well as increase competition from desirable species should be as important a component of weed control as is the application of control whether it be via biological, chemical, or mechanical methods.

4.1. Implications for wildland weed management

Experience with chemical and mechanical control suggests that vegetation response to reduction in weed biomass in native ecosystems will depend on factors such as the composition of seed banks and residual propagule availability, remnant community structure and composition, and the legacy effect of invasive plants on ecosystem processes such as nutrient supply (Cabin et al., 2000; D'Antonio et al., 1998; Walker and Lee, 2000; Denslow et al., unpublished) and disturbance history (Tunison et al., 2001). As in rangeland biocontrol projects, desired outcomes are most likely to be obtained using risk-benefit analyses that include identification of direct and indirect effects of target weed reduction and take into account the variation in impacts likely under heterogeneous habitat conditions. Higgins et al. (1997) provide

an example in their simulation model of the ecological and economic consequences of controlling alien plant invasions in the South African fynbos. An integrated approach using a variety of vegetation management techniques, rather than biocontrol alone, is most likely to lead to long-term maintenance of the community and ecosystem properties desired.

Reduction of disturbance and improvement of competition poses particular challenges in the management of wildlands. In Hawaii, the first priority for management of wet and moist forest reserves has been the removal of exotic ungulates (pigs, goats, cattle, mufflon sheep, and deer), thereby reducing grazing pressure on competing vegetation and, in the case of pigs, a major source of soil disturbance (Loope, 1992, 1998). Where disturbance is an integral part of the ecosystem, as in riparian communities, the opportunities for reinvasions will persist if exotic seed sources remain. And where productivity and growth rates are low, as in arid lands or in forest understory, the competitive pressure exerted by native species may be insufficient to prevent reestablishment of exotic pest species. Managers may need to couple use of biological control with chemical/mechanical applications to reduce exotic seed rain or spread of propagules from edges and trails. An effective use of biological control in the management of wildland weeds may be as a strategic supplement to other methods of control.

The control of *Melaleuca quinquenervia* in the South Florida Everglades ecosystem is a good example of careful assessment of the extent and impacts of the pest tree on community and ecosystem processes and the consistent application of integrated pest management approaches to the reduction of the pest (LaRoche, 1999). The first biological control agent, a snout beetle *Oxyops vitiosa* Pascoe (Coleoptera: Curculionidae), was released on *Melaleuca* in 1997. *Oxyops* reduces seed production and seedling survival (Center et al., 1999), depleting the seed bank, and improving the efficacy of chemical and mechanical control. Florida has succeeded in reducing the acreage under *Melaleuca* by a third in 10 years (LaRoche, 1999).

4.2. Future research approaches

The examples cited include a number of promising approaches to research on and evaluation of biological control projects to improve the likelihood of desirable outcome to target weed reduction. Advance assessment of sites targeted for weed reduction, including vegetation structure and composition, productivity, disturbance history, management objectives, and environmental heterogeneity, coupled with experimental reduction of target species, e.g., by chemical or mechanical means, and followed by post-control assessment of vegetation response will contribute to our ability to predict vegetation and nontarget plant responses to weed control.

Study designs that incorporate regional or environmental comparisons improve our ability to develop generalizations useful beyond single site studies. Use of risk/benefit analyses will stimulate identification of alternative outcomes, the consequences of habitat and climatic heterogeneity, and the economic feasibility of management alternatives. A variety of ecosystem process models can be employed productively to predict the consequences of control on hydrology, soil nutrient processes, fire-fuel characteristics, and other ecosystem processes.

Acknowledgments

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